

Displacement of diverse ichthyoplankton assemblages by a coastal upwelling event on the Sydney shelf

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ABSTRACT: The influences of upwelling-favourable winds and thermocline displacement on the distribution of temperate/tropical ichthyoplankton assemblages were determined from vertically stratified plankton hauls across the Sydney shelf, southeastern Australia. Five stations were sampled along a shore-normal transect off Sydney, Australia, on 3 or 4 consecutive nights during January and April 1994. High taxonomic diversity (111 ichthyoplankton families) was attributed to the convergence of temperate and tropical waters in this region. Total larval abundance was higher in January than in April, reflecting the spawning times of many coastal taxa. In both months, highest larval density and taxonomic diversity were associated with the interface between the mixed layer and the thermocline. In April, a period of upwelling-favourable winds resulted in the offshore displacement of the nearshore mixed layer, as well as numerous shelf-spawned larvae (e.g. *Centroberyx affinis*, *Chromis hypsilepsis*, *Arripis trutta*) from the nearshore region, and coincided with the injection of deeply distributed mesopelagic larvae into the nearshore zone (e.g. *Scopelosaurus* sp., *Melamphaes* sp.). Shelf-spawned larvae were displaced to the outer shelf, where they were still associated with the mixed layer/thermocline interface. Dynamic ichthyoplankton distributions are interpretable, at least at a scale of weeks, by considering larvae as tracers of the local hydrography.

KEY WORDS: Ichthyoplankton assemblages · Hydrography · Upwelling · Thermocline

INTRODUCTION

Planktonic distributions reflect local hydrographic patterns at many spatio-temporal scales. This biological-physical link is readily observed in the coastal ocean, where both physical and planktonic gradients tend to be steeper cross-shelf than along-shore (Richardson et al. 1980, Mackas 1984, Sabates 1990, McGowen 1993), and steeper vertically than horizontally (Ahlstrom 1959, Minami & Tamaki 1980, Boehlert et al. 1985). Studies of continental shelf ichthyoplankton communities have frequently been limited to an examination of either horizontal or vertical patterns, due to the high temporal variability encountered when sampling large spatial scales. The high amount of unexplained spatial and temporal variability which characterises many such studies may be a reflection of

variability in the unexplored dimension (e.g. Richardson et al. 1980, Sabates 1990, Cowen et al. 1993, Doyle et al. 1993, Loeb et al. 1993). In particular, studies of horizontal patterns are likely to be confounded by under-sampling of the relatively steep physical/biological vertical gradients associated with the pycnocline (Ahlstrom 1959, Loeb 1980).

The coastline of southeastern Australia is subject to considerable horizontal and vertical hydrographic variability as a result of large scale (10s of km), short term (days) upwelling events (McClellan-Padman & Padman 1991). This dynamic coastal ocean is also a convergence zone of tropical and temperate waters and, as a result, hosts a diverse adult fish community of temperate and tropical species (Kuitert 1993). The influence of sporadic, short term upwelling events on the distribution of ichthyoplankton over the shelf is unknown, despite their significance to environmental and fisheries studies. This situation arises partly from the diffi-

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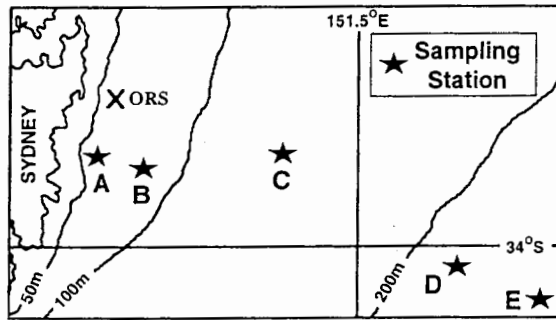


Fig. 1. Location of ichthyoplankton sampling stations (A to E) and Ocean Reference Station (ORS) across the Sydney continental shelf (Australia)

culties of sampling an unpredictable, large scale, short term oceanographic event.

Larval fish studies in the region have mostly been restricted to estuaries and the nearshore zone (Miskiewicz 1986, 1987, Steffe & Pease 1988, Steffe 1989, Gray et al. 1992, Gray 1993, 1996a, b, Kingsford & Suthers 1994). The only previous study of inner and outer shelf regions was restricted to surface observations and found that cross-shelf trends in neustonic ichthyoplankton reflected spawning patterns while, at smaller scales, ichthyoplankton variability reflected changes in near-surface hydrodynamics (Dempster et al. 1997). In surface and subsurface waters of the nearshore zone, consistent distributional trends occur with depth and distance from the shore, although high variability has been encountered in all directions (Gray 1993, 1996b). The vertical distribution of nearshore assemblages has not been related to hydrographic variability (thermocline depth), but rather to larval behaviour (Gray 1996a). Beyond the inner shelf, the composition and structure of subsurface Sydney shelf ichthyoplankton communities are not yet described. In addition, factors influencing both inner and outer shelf ichthyoplankton distributions are largely unknown, as is the case for many shelf regions.

The aim of the present study is to describe changes to shelf ichthyoplankton distributions which coincided with our observation of a coastal upwelling event off southeastern Australia. Based on observations made

elsewhere, it was predicted that ichthyoplankton variability during this event would closely reflect hydrographic variability at the same spatio-temporal scales. Our approach differs from many previous investigations of shelf ichthyoplankton assemblages in that we have concurrently considered cross-shelf and vertical distributional patterns, and compared these with hydrological gradients in the same dimensions.

METHODS

Location and time of study. Data were collected in continental shelf waters adjacent to Sydney, on the southeast coast of Australia (Fig. 1). The shelf off Sydney is 40 km wide, and the shelf break occurs at a depth of approximately 200 m. The dominant current in this region is the southward flowing East Australian Current (EAC) and associated eddies (Nilsson & Cresswell 1981). Local wind stress and the passage of coastally trapped waves result in regular reversals of the shelf and slope flow. Compared to along-shore currents, cross-shelf currents are small, usually $<10 \text{ cm s}^{-1}$ (Middleton, 1987). Density variability in the Sydney coastal ocean is primarily the result of changes in temperature (Griffin & Middleton 1992). Short term temperature change in shelf waters may be dramatic, particularly in the nearshore zone, where it is associated with local wind events, but also across the shelf and slope region as a result of intrusions of both warm and cold EAC eddies (Griffin & Middleton 1992, Gibbs et al. 1998). During summer, shelf waters generally exhibit strong temperature stratification, while during winter nearshore waters are often well mixed as a result of strong local winds and surface cooling (White & Church 1986).

Data were collected during two 10 d cruises, January and April 1994, aboard the research vessel 'Franklin'. On both cruises, data were collected from 5 stations along a cross-shelf transect. The transect began 2.7 km offshore and ended 40 km from the coast. Plankton sampling Stations A, B and C were within shelf waters (bottom depths less than 150 m). Stn D was at the shelf break (bottom depth 250 m), and Stn E occurred over the continental slope (bottom depth 600 m, Fig. 1, Table 1).

Table 1. Location, bathymetry and depth interval for each ichthyoplankton sampling station

Stn	Latitude	Longitude	Distance offshore (km)	Bottom depth (m)	Depth of sampling intervals (m)			
					Net 1	Net 2	Net 3	Surface
A	33° 56.7' S	151° 17.5' E	3	67	40–50	30–40	15–30	0–1
B	33° 57.5' S	151° 20.0' E	7	83	60–70	40–60	15–40	0–1
C	33° 57.0' S	151° 26.5' E	16	130	80–120	40–80	15–40	0–1
D	34° 00.0' S	151° 35.0' E	33	250	80–120	40–80	15–40	0–1
E	34° 02.5' S	151° 40.0' E	40	600	80–120	40–80	15–40	0–1

Plankton was collected on 22, 23 and 25 January and on the 5, 6, 7 and 8 April. Some locations were not sampled on 7 April due to bad weather. Plankton was collected at night between 20:30 and 05:00 h in January, and 19:00 and 06:00 h in April. Sunset and sunrise were at approximately 20:00 and 06:00 h in January, and 17:45 and 06:00 h in April, respectively.

Collection and processing of samples. Surface plankton samples were collected using a 75 × 75 cm square mouth net (330 µm mesh) fitted with a General Oceanics flow meter. Two surface hauls, each of 6 min duration, were conducted at each station. Near-surface temperature and salinity were recorded by shipboard instruments at a depth of 4 m.

Subsurface plankton samples were collected by a multiple, opening and closing net (an 'EZ net') with a square mouth of 1 m² and mesh size of 330 µm. The net was fitted with temperature, conductivity and depth sensors and 2 General Oceanics flow meters—one inside and one outside the net mouth. Real time data were communicated to an operator onboard ship who electronically triggered each net release. Three depth strata were sampled at each station, and actual sampling depths varied according to water depth at each station (Table 1). Subsurface haul durations were 10 min and obliquely sampled each depth stratum.

All plankton samples were immediately placed into seawater and 5 to 10% formaldehyde. Fish were removed from samples between 1 and 24 mo after collection, counted and identified to the lowest possible taxon and then stored in 95% ethanol. Results from surface sampling have been discussed in a previous paper by Dempster et al. (1997), but have been included here for comparison.

Nearshore wind and current data were obtained from the Ocean Reference Station (ORS), a permanent facility operated by Australian Water Technologies Ensign. The ORS records wind velocity and direction 5 m above the sea surface, and has current meters positioned at depths of 17 and 50 m. Water depth at this location is 65 m.

During daylight hours, a Neil-Brown CTD, with Turner fluorometer, was deployed along the sampling transect to provide additional cross-shelf hydrographic data (Gibbs et al. 1998). Fluorescence was uncalibrated, and measured as a percentage of full scale on the instrument.

Analysis. Composite cross-shelf temperature profiles from the EZ net CTD, over which ichthyoplankton abundance data were superimposed, were created for each monthly sampling.

The raw catches of total ichthyoplankton and of individual taxa were tabulated and then standardised to number of larvae per 100 m³. Standardised data were

used in all analyses. Mean density of total ichthyoplankton, mean number of ichthyoplankton families and mean densities of individual taxa were calculated for the 3 or 4 d of sampling at each sampling location during each sampling month.

Total ichthyoplankton density, number of families and densities of some individual taxa were illustrated for each sampling month. Taxa representative of a range of depth distributions were selected on the basis of their relative abundance and our ability to identify them to species. We could not, however, identify mesopelagic taxa to species. Local notosudids and melamphaeids are probably each represented by a single species (*Scopelosaurus meadi* and *Melamphaes* sp., Gomon et al. 1994) and are some of the few abundant, deeply distributed taxa. Myctophidae is a speciose family, but is a useful tracer of oceanic water at this taxonomic level (Cowen et al. 1993).

Similarities between average larval assemblages at each sampling location were analysed by multivariate analyses. Mean ichthyoplankton family abundances were fourth root transformed to enhance the contribution of less abundant taxa. Excluded from this analysis were those families which did not occur during both sampling times or contributed <1% to total abundance. As total larval densities differed by an order of magnitude between months, data were standardised to allow a comparison of sampling times. A Bray-Curtis similarity matrix was generated from this data (Bray & Curtis, 1957) and similarities between assemblages were graphically represented by non-metric multidimensional scaling (MDS, Clarke 1993).

Details of analysis of wind data may be found in Dempster et al. (1997).

RESULTS

Physical data and fluorescence

A southerly wind event (downwelling favourable) coincided with the commencement of sampling in January (Fig. 2). Also at this time, encroachment over the slope by a warm-core eddy produced shoreward, interior, Ekman transport over most of the shelf (Smith et al. 1999). A period of northeasterly winds (upwelling favourable) coincided with sampling in April (Fig. 2). The warm-core eddy was no longer adjacent to Sydney in April. Average, cross-shelf, current velocity between 4 and 6 April was approximately 0.02 m s⁻¹ (off-shore) at the ORS top current meter and approximately zero at the bottom current meter (M. Gibbs unpubl. data).

Highest chlorophyll concentrations over the shelf were repeatedly observed immediately below the

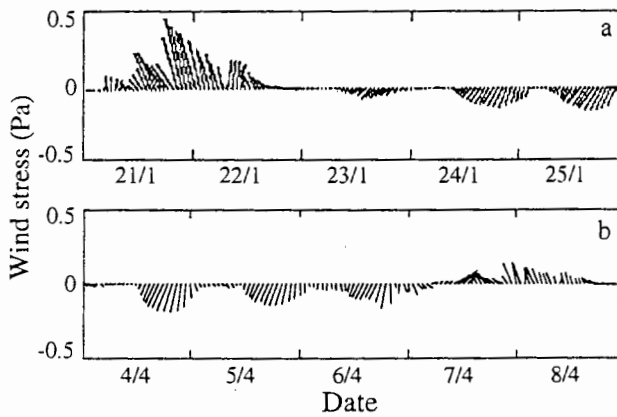


Fig. 2. Vector stick plots of hourly wind stresses at ORS from (a) 21 to 25 January and (b) 4 to 8 April 1994. (Vector sticks point in the direction in which wind was blowing)

mixed layer, at depths corresponding to the region of the upper thermocline, and changes in thermocline position corresponded to changes in the location of maximum fluorescence during each sampling period. This relationship is illustrated for 22 January (Fig. 3a, b).

The average cross-shelf temperature profile for the sampling period 22 to 26 January indicates a mixed layer (>23°C) of between 20 and 40 m depth was overlying a thermocline of approximately 50 m depth at each sampling station (Fig. 4). Shallow waters of Stns D and E were slightly warmer (>23.5°C), reflecting the near proximity of a warm-core eddy to the Sydney shelf (not shown).

The average cross-shelf temperature profile for the sampling period 5 to 8 April indicates hydrographic

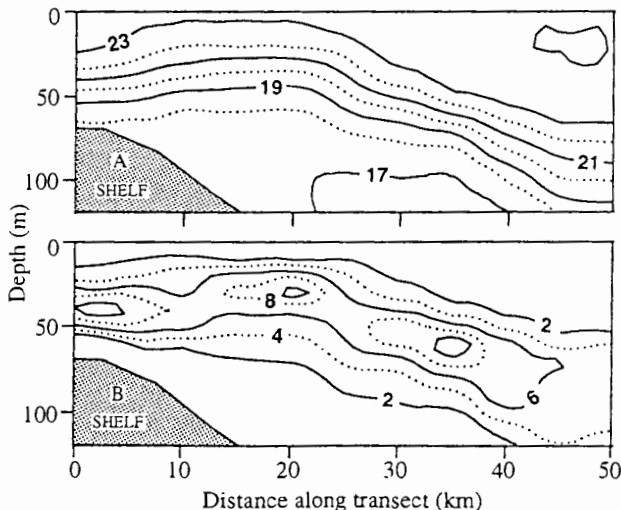


Fig. 3. Cross-shelf profiles of (a) temperature (°C) and (b) fluorescence (% of full scale on instrument) on 22 January 1994, illustrating the typical relationship between thermocline depth and depth of maximum fluorescence off Sydney

conditions of the nearshore region were different to those of the outer shelf and slope during this second sampling period (Fig. 4). At Stns A and B, the mixed layer (>23°C) was displaced by coastal upwelling of cooler shelf water. At Stns C to E, a mixed layer of 40 m depth presented hydrographic conditions similar to those occurring over the shelf in January. The stratified region underlying the mixed layer in April (hereafter referred to as the 'thermocline') extended to a depth of approximately 130 m in offshore waters (not shown).

Total larval abundance and diversity

Total abundance and diversity of fish larvae captured in January was greater than in April. In 3 nights of sampling in January, 26866 larvae representing 99 families were captured. In 4 nights of sampling in April, 23915 larvae representing 95 families were captured (Table 2). Thus, the average ichthyoplankton catch per night in January was approximately 1.5 times higher than it was in April.

In January, approximately 75% of the total catch was comprised of 4 families—Myctophidae, Carangidae, Gonostomatidae and Clupeidae. In April, 12 taxa contributed 75% of the total catch—Myctophidae, *Gonorhynchus greyi*, Serranidae, *Centroberyx affinis*, leptocephali larvae, Scorpaenidae, Carangidae, Gonostomatidae, Callionymidae, Sillaginidae, Platycephalidae and Cepolidae (Table 2). In January (and April), 80% (90%) of carangids captured were *Trachurus novaezelandiae*, 66% (64%) of gonostomatids were *Cyclothone* spp. and 75% (64%) of sillaginids were *Sillago flindersi* (Table 3). The composition of the clupeid catch varied between months, being 65 and 32% *Hyperlophus vittatus* and *Sardinops neopilchardus*, respectively, in January and 28 and 58% *H. vittatus* and *Etrumeus teres*, respectively, in April. In other abundant families, either no single species was dominant or individuals were too small to be identified beyond the family level. Most larvae captured during the study were at a preflexion or flexion stage of development, with few postflexion individuals encountered.

The average number of ichthyoplankton families per sample decreased with distance from shore in January but increased with distance from shore in April (Fig. 4a, b). The number of families per sample ranged between 5 and 41 in January, and 0 and 44 in April. In both months, the number of families encountered was relatively low at the surface and in deep samples, and tended to be highest in shallow and middle depth samples, and corresponded to regions within the mixed layer and thermocline.

Highest densities of ichthyoplankton occurred at either end of the sampling transect in January (Fig. 4c). Larval densities during January ranged between 8 and 3180 larvae 100 m^{-3} . In April, average densities were much lower, ranging between 0 and 141 larvae 100 m^{-3} , and densities increased with increasing distance from shore (Fig. 4d). Ichthyoplankton density at the surface and at the deepest locations was low in both months, except at Stn E in April, due to the presence of relatively high numbers of *Gonorhynchus greyi* in surface waters at this time (see Fig. 6f). Most of the cross-shelf variability in larval density occurred at shallow and middle sampling depths.

Changes in larval densities corresponded to changes in the depth of the mixed layer. In January, shallow depth samples contained highest densities of larvae at all stations across the shelf (Fig. 4c). These shallow samples were taken primarily from within mixed layer water, at both inshore and offshore stations. In April, the depth of the mixed layer decreased at inshore stations such that all nearshore subsurface sampling was beneath the mixed layer (Fig. 4d). Nearshore larval densities were relatively low at all sampling depths in April. In contrast, the depth of the mixed layer increased slightly at offshore stations, which corresponded to an increase in larval density at middle sample depths, relative to densities at other depths.

Distributions of individual taxa

Most of the abundant taxa encountered during the study exhibited a change in cross-shelf distribution between sampling times. In particular, much of the between-month variability in total ichthyoplankton density and in the distribution of ichthyoplankton families was related to large between-month changes in the distribution of shelf-spawned taxa. Some shelf-spawned taxa, which had been abundant in the nearshore zone during January, were largely absent from all stations in April (e.g. clupeids and engraulids, Table 2). Of the shelf-spawned taxa which occurred in both months, many were abundant at inshore stations during January, but at offshore stations during April (e.g. *Centroberyx affinis*, *Chromis hypsilepsis* and *Arripis trutta*, Table 2, Fig. 5). Larvae which were abundant at offshore stations in January were predominantly mesopelagic (not shelf-spawned) and were again encountered in the offshore region during April (e.g. myctophids, Table 2, Fig. 6).

In January, the larvae of *Centroberyx affinis*, *Chromis hypsilepsis* and *Arripis trutta* were abundant at inshore Stns A to C, particularly in samples from within the mixed layer and upper thermocline (Fig. 5a-c). In

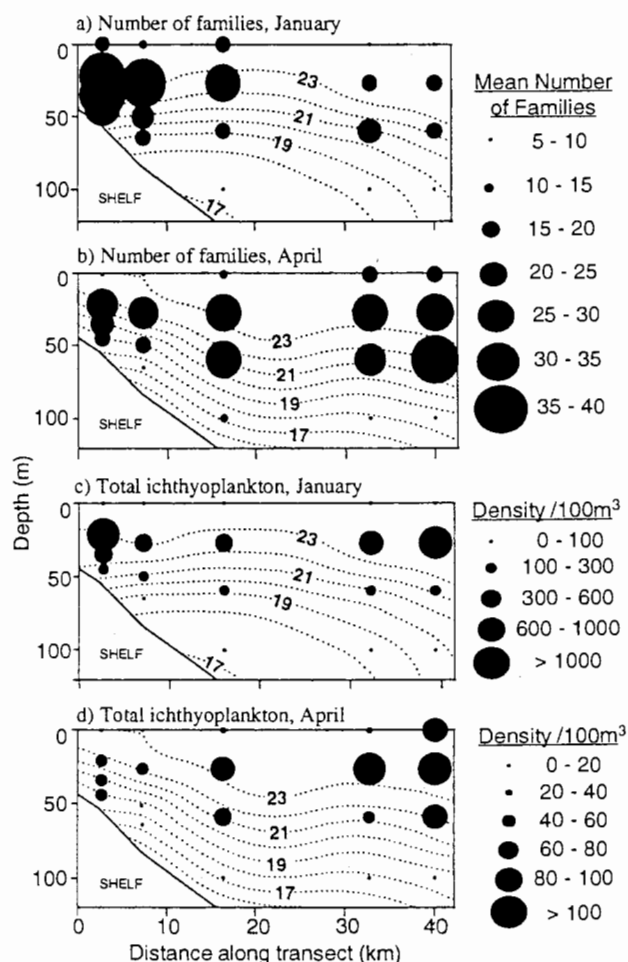


Fig. 4. Mean number of families caught at night in (a) January and (b) April 1994, and mean density of total ichthyoplankton in (c) January and (d) April 1994. Circle size is proportional to mean number of families (or ichthyoplankton density) at each sampling location and circles are centred in the middle of each sampling depth interval. Isotherms indicate average temperature profile during each sampling period

April, however, these larvae were most abundant at offshore Stns C to E, again occurring within the mixed layer and upper thermocline (Fig. 5d-f). This represented an offshore shift in the location of maximum density of these larvae.

An offshore shift in maximum density was also observed in taxa which were already abundant at offshore stations in January. The larvae of *Gonorhynchus greyi* and myctophids were abundant in surface/mixed layer and mixed layer/upper thermocline samples, respectively, across the shelf and slope in January, although tending to be most abundant offshore at Stns D and E (Fig. 6a, b). In April, these larvae were again most abundant offshore, now at Stn E, but were present in relatively low densities at inshore Stns A and B (Fig. 6e, f).

Table 2. Summary of total raw (non-standardised) catch of fish larvae caught across the Sydney shelf in January and April 1994. Listed is contribution (%) of each family to the total monthly catch of larvae and a monthly ranking in order of decreasing contribution to total monthly catch. Refer to Table 3 for specific details of families containing several identified species. Classification follows Eschmeyer (1990). -: no larvae

Order	Family	Specific	Contribution of family to total abundance		Abundance ranking	
			Jan	Apr	Jan	Apr
Anguilliformes	Leptocephali		1.63	6.77	9	5
Clupeiformes	Clupeidae	(See Table 3)	5.24	0.29	4	33
	Engraulidae	<i>Engraulis australis</i>	1.38	0.15	10	41
Gonorhynchiformes	Gonorhynchidae	<i>Gonorhynchus greyi</i>	0.16	13.52	30	2
Salmoniformes	Argentiniidae		0.04	0.16	56	38
	Bathylagidae	<i>Bathylagus</i> spp.	-	0.02	-	71
Stomiiformes	Gonostomatidae	(See Table 3)	10.57	3.12	3	8
	Stomiidae	<i>Stomias</i> spp.	-	<0.01	-	89
	Astronesthidae		0.01	0.09	81	48
	Melanostomiidae		0.05	0.06	52	55
Aulopiformes	Idiacanthidae	<i>Idiacanthus</i> spp.	-	<0.01	-	90
	Aulopidae	<i>Aulopus</i> spp.	0.07	1.02	45	20
	Notosudidae	<i>Scopelosaurus</i> spp.	0.05	0.29	50	34
	Synodontidae	<i>Synodus</i> spp.	0.52	0.20	15	36
	Evermannellidae		0.01	<0.01	82	91
	Paralepididae	(See Table 3)	0.36	0.11	19	42
	Chlorophthalmidae	<i>Chlorophthalmus</i> spp.	<0.01	-	93	-
Scopelarchidae		0.01	-	83	-	
Myctophiformes	Myctophidae		31.09	16.47	1	1
Gadiformes	Bregmacerotidae		0.10	0.10	41	44
	Moridae		0.14	0.28	36	35
	Merlucciidae		0.01	0.54	84	24
	Gadidae		0.02	-	74	-
Ophidiiformes	Ophidiidae	(See Table 3)	0.01	0.05	75	57
	Carapidae		0.02	0.16	69	39
Lophiiformes	Antennariidae		0.01	0.02	76	74
	Ceratiidae		0.05	0.20	51	37
Gobiesociformes	Gobiesocidae	(See Table 3)	0.13	0.01	38	88
Lampridiformes	Trachipteridae		0.03	0.02	65	75
Beloniformes	Exocoetidae		0.01	0.01	85	82
	Bellonidae		-	<0.01	-	92
	Scomberesocidae	<i>Scomberesox saurus</i>	0.04	0.01	57	83
Beryciformes	Trachichthyidae		0.04	0.07	58	53
	Berycidae	<i>Centroberyx affinis</i>	2.80	8.80	5	4
	Holocentridae		0.01	-	88	-
	Melamphaeidae		0.04	0.36	59	29
	Unidentified		<0.01	-	94	-
Zeiformes	Caproidae		<0.01	0.08	95	51
Syngnathiformes	Macroramphosidae	<i>Macroramphosus scolopax</i>	0.02	1.95	70	14
	Fistularidae	<i>Fistularia</i> spp.	0.01	-	86	-
	Syngnathidae		-	<0.01	-	93
Scorpaeniformes	Scorpaenidae	(See Table 3)	0.42	4.14	17	6
	Triglidae		0.73	0.40	13	26
	Platycephalidae		2.22	2.23	8	11
	Hoplichthyidae	<i>Hoplichthys</i> spp.	-	<0.01	-	94
	Dactylopteridae		0.04	0.04	60	63
Perciformes	Howellidae	<i>Howella</i> spp.	0.28	0.11	21	43
	Ambassidae	<i>Ambassis</i> spp.	0.15	0.02	33	76
	Acropomatidae		0.01	0.02	90	77
	Serranidae		0.04	9.14	61	3
	Pseudochromidae		-	0.01	-	80
	Callanthiidae	<i>Callanthias</i> spp.	-	0.08	-	49
	Terapontidae	<i>Pelates sexlineatus</i>	0.01	0.03	89	65
	Apogonidae	(See Table 3)	0.20	0.46	27	25
	Sillaginidae	(See Table 3)	2.40	2.63	7	10
	Malacanthidae		-	0.06	-	56

Table 2 (continued)

Order	Family	Specific	Contribution of family to total abundance		Abundance ranking	
			Jan	Apr	Jan	Apr
Perciformes (continued)	Carangidae	(See Table 3)	26.80	3.81	2	7
	Coryphaenidae	<i>Coryphaena</i> spp.	0.09	<0.01	43	95
	Bramidae		0.01	0.01	77	84
	Arripidae	<i>Arripis trutta</i>	0.18	0.30	29	32
	Lutjanidae		0.02	-	71	-
	Gerreidae	<i>Gerres</i> spp.	0.39	0.03	18	67
	Haemulidae		-	0.08	-	52
	Sparidae	(See Table 3)	0.05	0.34	53	30
	Lethrinidae		0.01	-	91	-
	Nemipteridae		0.01	0.01	78	79
	Sciaenidae		0.22	0.10	25	45
	Mullidae		0.25	0.82	22	22
	Pemppheridae		0.14	0.03	34	66
	Kyphosidae	<i>Kyphosus</i> spp.	0.15	0.04	31	61
	Scorpididae		0.07	0.03	46	68
	Girellidae	<i>Girella</i> spp.	0.15	-	32	-
	Monodactylidae	<i>Schuetta</i> spp.	0.19	0.05	28	58
	Chaetodontidae		0.01	0.01	92	78
	Pomacentridae	(See Table 3)	2.55	1.41	6	16
	Cirrhitidae		0.02	-	72	-
	Aplodactylidae		<0.01	-	96	-
	Cheilodactylidae		<0.01	1.00	97	21
	Cepolidae		0.23	2.11	24	12
	Mugilidae		0.22	0.39	26	27
	Labridae		0.99	0.74	12	23
	Odacidae		<0.01	0.16	98	40
	Scaridae		0.06	0.08	47	50
	Chiasmodontidae		0.06	0.06	48	54
	Champsodontidae		0.01	0.09	87	47
	Uranoscopidae		<0.01	0.01	99	81
	Creedidae	(See Table 3)	0.31	1.35	20	17
	Leptoscopidae		<0.01	-	103	-
	Percophidae		0.06	2.10	49	13
	Pinguipedidae	<i>Parapercis</i> spp.	0.03	1.31	64	19
	Tripterygiidae		<0.01	-	101	-
	Blennidae		0.04	0.04	55	64
	Callionymidae		0.44	3.02	16	9
	Schindleriidae	<i>Schindleria</i> spp.	0.05	0.01	54	86
	Gobiidae		0.69	1.33	14	18
	Microdesmidae		<0.01	-	100	-
	Siganidae		-	0.01	-	85
	Acanthuridae		0.03	-	63	-
	Sphyraenidae	<i>Sphyraena</i> spp.	0.03	0.05	66	59
	Gempylidae		0.04	0.03	62	69
	Trichiuridae	<i>Lepidopus</i> spp.	<0.01	0.02	102	72
	Scombridae		0.11	0.05	40	60
	Nomeidae		0.09	0.02	42	73
Tetraodonidae	<i>Tetraodonurus</i> spp.	0.14	0.01	35	87	
Pleuronectiformes	Paralichthyidae		0.25	0.39	23	28
	Bothidae		1.23	1.49	11	15
	Pleuronectidae		0.01	0.03	79	70
	Soleidae		0.02	0.10	73	46
	Cynoglossidae		0.13	0.34	39	31
Tetraodontiformes	Unidentified		0.03	-	67	-
	Monacanthidae		0.13	-	37	-
	Ostraciidae		0.03	<0.01	68	96
	Tetraodontidae		0.07	0.04	44	62
	Diodontidae		-	<0.01	-	97
Unidentified	Unidentified		0.01	-	80	-
			1.90	2.27	Not ranked	

Total ichthyoplankton catch: Jan = 26 866; Apr = 23 915; Jan + Apr = 50 781

No. of ichthyoplankton families caught (excluding leptocephali larvae): Jan = 103; Apr = 95; Jan + Apr = 111

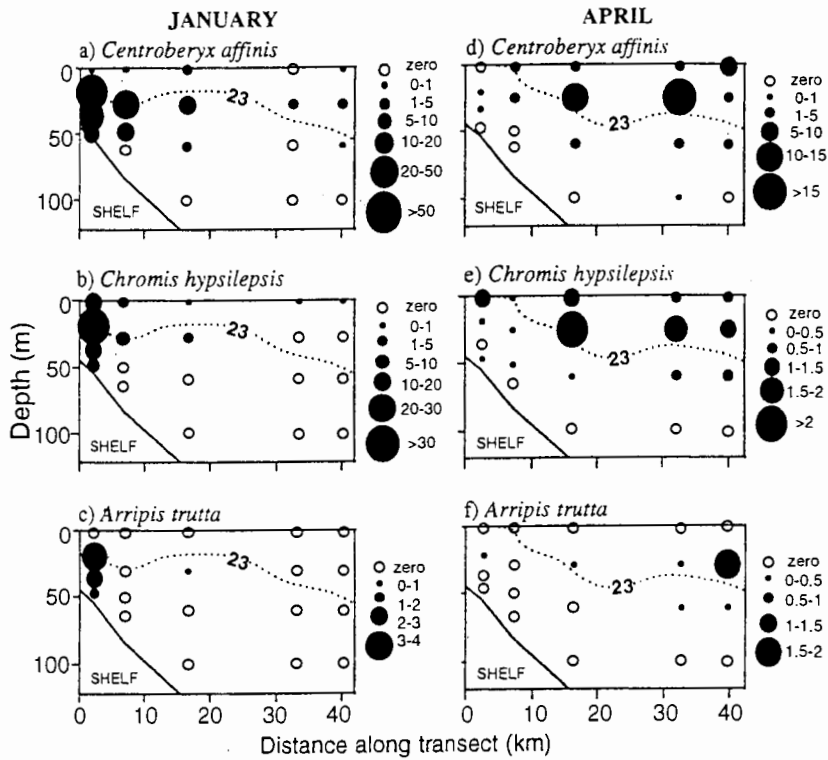


Fig. 5. Mean night-time densities of (a, d) *Centroberyx affinis*, (b, e) *Chromis hypsilepsis* and (c, f) *Arripis trutta* in January and April 1994. Circle size is proportional to mean density at each sampling location and circles are centred in the middle of each sampling depth interval. 23°C isotherm indicates average depth of mixed layer during each sampling period

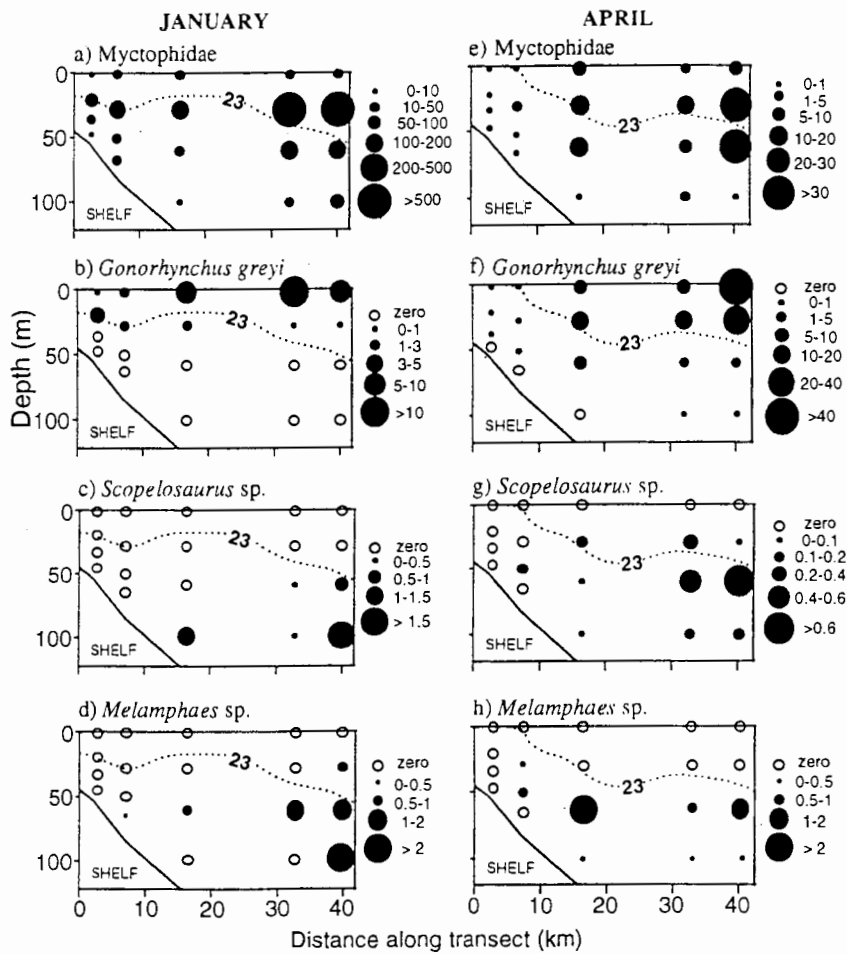


Fig. 6. Mean night-time densities of (a, e) *Myctophidae*, (b, f) *Gonorhynchus greyi*, (c, g) *Scopelosaurus* sp. and (d, h) *Melamphaes* sp. in January and April 1994. Circle size is proportional to mean density at each sampling location and circles are centred in the middle of each sampling depth interval. 23°C isotherm indicates average depth of mixed layer during each sampling period

Table 3. Catches of ichthyoplankton families consisting of several identified taxa. Listed is the specific contribution (%) to the total monthly family catch. *Calculated from subsurface samples only

Family	Specific	% of family abundance*	
		Jan	Apr
Clupeidae	<i>Hyperlophus vittatus</i>	65.3	28.4
	<i>Sardinops neopilchardus</i>	32.3	11.9
	<i>Etrumeus teres</i>	0.4	58.2
	Unidentified spp.	2.0	1.5
Gonostomatidae	<i>Cyclothone</i> spp.	66.0	64.5
	<i>Diplophos</i> spp.	1.9	0.0
	<i>Mauroliticus</i> spp.	0.0	0.0
	<i>Vinciguerria</i> spp.	0.3	0.0
	Unidentified spp.	31.8	35.5
Paralepididae	<i>Studis atrox</i>	4.1	0.0
	<i>Notolepis</i> spp.	1.0	7.4
	<i>Stemonosudis</i> spp.	1.0	0.0
	Unidentified spp.	93.8	92.6
Ophidiidae	<i>Genypterus blacodes</i>	33.3	45.5
	Unidentified spp.	66.7	54.6
Gobiesocidae	<i>Alabes</i> spp.	76.5	100.0
	Unidentified spp.	23.5	0.0
Scorpaenidae	<i>Neosebastes</i> spp.	13.9	3.8
	<i>Centropogon australis</i>	11.9	1.8
	<i>Helicolenis</i> spp.	0.0	0.1
Apogonidae	<i>Apogonops anomalus</i>	47.9	97.3
	Unidentified spp.	52.1	2.7
Sillaginidae	<i>Sillago flindersi</i>	74.6	63.7
	<i>Sillago</i> spp.	25.4	36.3
Carangidae	<i>Trachurus novaezelandiae</i>	80.3	90.5
	<i>Pseudocarynx dentex</i>	19.5	7.4
	<i>Seriola</i> spp.	0.0	1.5
	Unidentified spp.	0.2	0.7
Sparidae	<i>Rhabdosargus sarba</i>	8.3	53.1
	<i>Acanthopagrus australis</i>	8.3	25.9
	<i>Pagrus auratus</i>	50.0	19.8
	Unidentified spp.	33.3	1.2
Pomacentridae	<i>Chromis hypsilepsis</i>	93.4	87.6
	Unidentified spp.	6.6	12.4
Creedidae	<i>Creedia haswelli</i>	90.2	100.0
	Unidentified spp.	9.8	0.0

The larvae of some more deeply distributed taxa underwent an onshore shift in the location of maximum density between sampling times. The distributions of *Scopelosaurus* sp. and *Melamphaes* sp. larvae were mostly restricted to deep water over the outer shelf and slope in January, but extended into the nearshore zone in April (Fig. 6c, d, g, h).

The inshore occurrence of these deeply distributed larvae, which were formerly restricted to the outer shelf, corresponded to the coastward intrusion of cold, deep, shelf water. Similarly, the disappearance in April of both shelf-spawned and mesopelagic larvae from shallow, nearshore waters corresponded to the offshore displacement of the nearshore mixed layer by upwelled water.

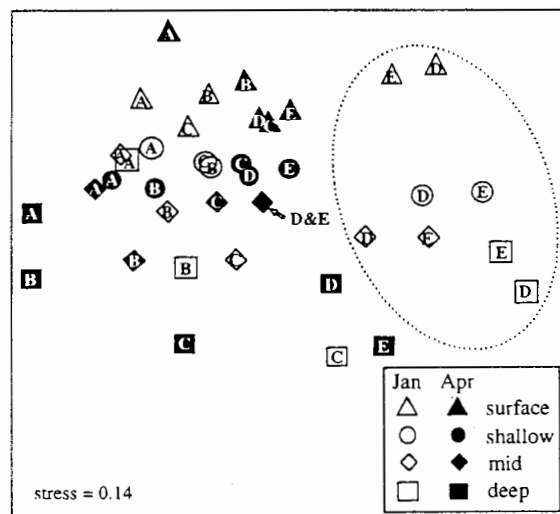


Fig. 7. Two dimensional, MDS ordination of Bray-Curtis similarities between average ichthyoplankton assemblages at each sampling location in January and April 1994. Each point within the ordination represents the average assemblage at each depth/station location in either January or April. Letters indicate stations. Data were standardised and 4th root transformed; taxa excluded if not occurring in both months or if contributing <1% of total abundance

Similarities between ichthyoplankton assemblages

The nearshore upwelling event during April coincided with changes to the distribution of ichthyoplankton assemblages across the shelf. The MDS ordination of average assemblages at each sampling location, from both sampling times, indicated that assemblages from Stns D and E in January (circled) are distinct from all other assemblages (Fig. 7). In April, assemblages sampled at D and E were similar to those sampled further inshore during both January and April. The dimensions of the ordination may be interpreted as depth (top-bottom) and distance from shore (left-right). On both sampling occasions, surface assemblages are at the top of the ordination, deep are at the bottom, inshore are to the left, and offshore are to the right. The between-month shift in the positions of Stns D and E assemblages was to the left, suggesting the character of outer shelf and slope communities became more 'coastal' between April and January.

DISCUSSION

Taxonomic diversity of the Sydney shelf

The Sydney shelf ichthyoplankton community is taxonomically diverse. During 7 nights of sampling, 111 families (excluding leptocephali larvae) were col-

lected, with up to 44 families collected by a single 10 min tow. Previous ichthyoplankton surveys of coastal and shelf regions elsewhere report lower diversity, e.g. 101 families in 33 yr of sampling off California (Moser et al. 1993, 1994), 100 families in 33 d in the Gulf of Mexico (Richards et al. 1993), 103 families in 1 yr off northwestern Australia (Young et al. 1986) and 99 families in 3 yr on the Australian Great Barrier Reef (Leis & Goldman 1987). The high diversity may be due, in part, to the fact that the Sydney shelf is adjacent to a region of convergence between temperate and tropical waters and assemblages may have included fauna of both water types. The presence during this study of taxa such as scarids and fistulariids, which are usually associated with coral reefs (Leis & Rennis 1983), indicates the southward advection of tropical species.

Warm-core eddies and meanders, associated with the EAC, have the potential to transport tropical organisms southward into temperate zones. The EAC originates in the Coral Sea and flows southward along the east Australian coast to approximately 32° S, where it then turns eastward. In this region, several warm-core eddies may form each year and individual eddies may persist for over 12 mo (Nilsson & Cresswell 1981). These eddies may continue moving southward and frequently encroach over the continental slope and shelf. For example, during the January sampling period, an intense warm-core eddy was present on the continental slope adjacent to Sydney. Previous ichthyoplankton surveys on the southeast Australian coast have encountered the larvae of tropical species in temperate waters (Miskiewicz 1989, Gray 1993) and juveniles of tropical species regularly recruit to temperate coastal habitats as far south as 35° S, although survival of these individuals is generally restricted to the warmer months (Leadbitter & Pollard 1987, Kuitert 1993). The transport of tropical species by warm currents and eddies into temperate habitats has been documented elsewhere, including Western Australia (Maxwell & Cresswell 1981, Hutchins & Pearce 1994) and northeastern America (Cowen et al. 1993). The subsequent mortality of such individuals suggests that larvae become entrained by chance and are transported passively within the warm water mass.

Tracers of water movement

The distribution of total ichthyoplankton abundance and diversity showed different cross-shelf trends in each month. In January, abundance was highest at either end of the sampling transect and diversity decreased with distance from shore. In April, both abundance and diversity increased with distance from shore. Changes in the distribution of shelf-spawned

larvae account for much of this variability. Numerous taxa which had been very abundant within the inshore region in January either largely disappeared or were captured further offshore in April. Several processes, biological and physical, were responsible for these dramatic changes.

Firstly, a period of upwelling-favourable winds, and the subsequent offshore displacement of warm surface water, observed during April appeared to markedly alter the distribution of ichthyoplankton over the shelf. During both sampling periods, maximum ichthyoplankton density and taxonomic diversity occurred within the warm water of the mixed layer and the adjacent, cooler, stratified water of the upper thermocline. In the absence of an overlying mixed layer, such as occurred in the nearshore zone in April, relatively low ichthyoplankton density and diversity were associated with stratified water. This result suggests an association of numerous coastal and mesopelagic larvae with waters of the mixed layer. Upwelling-favourable winds observed in April appeared to displace both the mixed layer and its associated ichthyoplankton community offshore. At this scale, larvae appear as tracers of water movement over the shelf.

This result is complemented by between-month changes in the distribution of deeper larvae, such as *Scopelosaurus* sp. and *Melamphaes* sp. Just as coastal upwelling implies the offshore transport of surface water, it also implies the shoreward transport of deeper water. The distributions of these taxa moved shoreward between January and April, corresponding to the concurrent, shoreward movement of deeper water. Thus, these more deeply distributed larvae are also apparent tracers of water movement over the shelf.

Secondly, the general decline in the density of shelf-spawned larvae between sampling periods and the near absence in April of taxa such as clupeids and engraulids, which had been abundant in January, probably reflect seasonal spawning patterns. Many local coastal species, including clupeids, engraulids, sillaginids, *Centroberyx affinis* and *Arripis trutta*, spawn during summer and the April sampling period probably coincided with the end of the spawning periods of these taxa (Kailola et al. 1993). In contrast to coastal fish, the reproductive cycles of many mesopelagic fish are weakly seasonal, or non-seasonal (Gjosæter & Kawaguchi 1980, Olivar & Beckley 1994), resulting in less pronounced seasonal variability in the composition of many offshore (mesopelagic) ichthyoplankton communities (Ahlstrom 1972, Loeb 1979, Doyle et al. 1993). The composition of offshore communities sampled by this study displayed limited between-month variability.

Further biological factors could have affected the observed change in distributions. For example, a shift

in adult spawning location could result in differing larval distributions. The spawning location(s) of most species encountered in this study, including abundant larval species such as *Centroberyx affinis*, is not known. However, *Arripis trutta* spawns pelagic eggs in the nearshore zone along the southeast Australian coast (Kailola et al. 1993) and *Chromis hypsilepsis* lays demersal eggs in the nearshore zone (Kuitert 1993). Despite restricted and consistent spawning locations, larvae of these species underwent a major distributional shift between months, suggesting that spawning location was not a significant factor influencing distributional variability in these larvae.

The mechanism(s) by which planktonic larvae maintain their distributions is unclear. The results of the present study suggest that ichthyoplankton communities in the Sydney region may be modelled as passive tracers of water mass movement, but the processes leading to such distributions may be physical, behavioural, or a combination of both. The concurrent displacement of fish larvae and water could arise if larvae were drifting passively within their host water masses but could also arise through active behavioural responses to changes in hydrography. Oceanographic processes have the potential to retain or transport passive particles, and hence also larvae (Norcross & Shaw 1984, Kingsford 1990, Sabates & Maso 1992, Govoni & Pietrafesa 1994), yet most ichthyoplankton are not completely passive particles. Swimming ability may be limited in young larvae, such as those encountered in this study (Miller et al. 1988), although buoyancy adjustment could allow considerable vertical and horizontal migration, even in very young larvae. Evidence from numerous studies suggests that plankton distributions are often defined by hydrodynamic boundaries but may be maintained by plankton behaviour. Many planktonic organisms appear capable of moving between water masses, and do so at certain times in their life history, but are equally capable of maintaining their distributions within the same water mass or frontal region, perhaps by using hydrological parameters as a guide (e.g. Sameoto 1984, Sinclair & Iles 1985, Boucher et al. 1987). In addition, planktonic distributions do not always follow the predicted path of 'passive particles' and behavioural mechanisms must sometimes be invoked (Cowen et al. 1993, Wiafe & Frid 1996). Thus, it may be appropriate to consider planktonic organisms as 'active' tracers. Their distributions frequently reflect hydrological boundaries, in the character of passive particles, but behavioural mechanisms may underlie such distributions. Determination of the exact nature of the mechanisms which influence larval distributions in the Sydney region requires sampling at a greater frequency and smaller spatial scale than that undertaken by the present study.

Interface between mixed layer and thermocline

Highest ichthyoplankton density and diversity were typically associated with the interface between the mixed layer and the thermocline over the Sydney shelf. Thermocline, or halocline, position frequently appears to regulate the vertical distribution of ichthyoplankton in coastal and oceanic waters (Ahlstrom 1959, Loeb 1980, Kendall & Naplin 1981, Boehlert et al. 1985, Davis et al. 1990, Palomera 1991). Maximum chlorophyll concentrations were also observed adjacent to this interface, within the upper thermocline. The interface between the warm, mixed layer and the cooler thermocline may represent a region of optimum growth and feeding for many larvae.

In contrast to our results, Gray (1996a) concluded that variations in thermocline depth did not contribute to the structure of nearshore ichthyoplankton assemblages off Sydney, and that the vertical distribution of nearshore ichthyoplankton in months of water column stratification was similar to that in a month in which there was no stratification. Differing hydrodynamic regimes may account for such contrasting conclusions. Our study found that, when compared to conditions elsewhere over the shelf, the nearshore mixed layer and thermocline were often poorly defined and stratification of the nearshore water column was in a constant state of flux (changing daily). Stratification of the nearshore zone (0 to 5 km from shore) is primarily driven by, and rapidly responsive to, wind forcing, unlike regions further offshore, which are primarily driven by currents (Gibbs et al. 1998). Hydrodynamics in the nearshore zone are thus fundamentally different to those elsewhere over the shelf. It may be that the hydrodynamic instability of the nearshore zone inhibits the formation of ichthyoplankton distributions which are typical elsewhere over the shelf. Alternatively, the behavioural response of nearshore ichthyoplankton communities to hydrodynamic variability may be different to that of communities further offshore (Marliave 1986, Lavett Smith et al. 1987).

Conclusions

The response of ichthyoplankton to coastal upwelling, as presented here, is based on our observations of a single oceanographic event. The generality of the response in the Sydney region can only be determined by further sampling of future upwelling events. Unfortunately, the unpredictable and transient nature of many coastal processes, including upwelling, tends to limit the number of observations which can be made. However, similar ichthyoplankton responses to coastal upwelling have been seen elsewhere (e.g.

Hamann et al. 1981), suggesting that the observations presented here may be typical.

Irregular, unpredictable and dramatic changes in coastal hydrography, such as that observed in April 1994, and the concurrent changes in ichthyoplankton distributions, may confound attempts to describe ichthyoplankton distributions in the coastal ocean. Indeed, previous ichthyoplankton studies in the Sydney region have encountered high biological variability at a range of temporal and spatial scales, which was not adequately explained by non-hydrological parameters such as sampling depth, distance from shore, ontogenetic changes in distribution and seasonal reproductive cycles (Gray et al. 1992, Gray 1993, 1996b). The results of the present study confirm the need for adequate physical data to complement biological sampling programmes. In the absence of hydrographic information, the distributional variability observed in this study would have been difficult to interpret. Further insights into the influence of physical forcings on ichthyoplankton distributions may be gained by the examination of among-night variation (Smith et al. 1999).

The results of this study indicate that the vertical structure of ichthyoplankton communities is influenced by the positioning of hydrographic boundaries, especially the interface between the mixed layer and the thermocline. Results also suggest horizontal structuring of assemblages, despite the absence of any obvious hydrographic gradient in this dimension. Specifically, the community associated with the mixed layer during January showed cross-shelf trends in taxonomic composition, which reflected general spawning locations. In the nearshore zone, shelf-spawned taxa were dominant, whereas over the outer shelf and slope, mesopelagic taxa were dominant. However, while some mesopelagic larvae were also present in the nearshore zone, shelf-spawned taxa were largely absent from offshore regions during January. A similar pattern has been observed across the Spanish continental shelf, in association with a salinity front (Sabates & Olivar 1996). The mechanism on the Sydney shelf which temporarily restricts the offshore distribution of coastal larvae, while allowing the shoreward movement of oceanic larvae, is not clear from this study and presents an area for future research.

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